Odocoileus virginianus. By Winston Paul Smith

Odocoileus Rafinesque, 1832

Cervus Erxleben 1777:294 (part). Not *Cervus* Linnaeus, 1758.

Dama Zimmermann, 1780:129. Type species *Dama virginiana* Zimmermann. Not *Dama* Frisch (China, 1960).

Mazama Hamilton-Smith, 1827b:314. Proposed as a subgenus of *Cervus*; no type species designated; preoccupied by *Mazama* Rafinesque, 1817.

Odocoileus Rafinesque, 1832:109. Type species *Odocoileus speleus* Rafinesque, by monotypy.

Dorcelaphus Gloger, 1841:140. No type species designated.

Cariacus Lesson, 1842:173. Proposed as a "groupe" (subgenus) of *Cervus*; no type species designated.

Oplacerus Haldeman, 1842:188. Replacement name for *Mazama* Hamilton-Smith, 1827a, preoccupied by *Mazama* Rafinesque.

Reduncina Wagner, 1844:373. Proposed as a subgenus of *Cervus*; no type species designated.

Macrotis Wagner, 1855:368. Proposed as a subgenus of *Cervus*; type species *Cervus macrotis* Say, 1823 by tautonomy; preoccupied by *Macrotis* Dejean, a genus of Coleoptera and by *Macrotis* Reed, a genus of marsupials.

Eucervus Gray, 1866:338. Type species *Cervus macrotis* Say, by subsequent designation (Miller, 1924).

Coassus Gray, 1874:332 (part). Used as a subgenus, not *Coassus* Gray, 1843.

Otelaphus Fitzinger, 1874:356. Replacement name for *Macrotis* Wagner.

Gymnotis Fitzinger, 1879a:343. Type species *Gymnotis wiegmanni* Fitzinger, by monotypy.

Mamcariacus Herrera 1899:29. A formula, not a name and has no status in nomenclature (Melville, 1984).

Odocoelus G. M. Allen, 1901:449. Unjustified emendation of *Odocoileus* Rafinesque.

Odontocoelus Sclater, 1902:290. Unjustified emendation of *Odocoileus* Rafinesque.

Palaeoodocoileus Spillmann, 1931:30. Type species *Palaeoodocoileus abeli* Spillmann, by original designation.

Protomazama Spillmann, 1931:42. Type species *Protomazama aequatorialis* Spillmann, by monotypy.

Aplacerus Hall and Kelson, 1959:1003. Incorrect subsequent spelling of *Oplacerus* Haldeman.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Family Cervidae, Subfamily Odocoileinae. *Odocoileus* includes two extant species, *O. virginianus* and *O. hemionus* (Hall, 1981).

Odocoileus virginianus (Zimmermann, 1780)

White-tailed Deer

Dama virginiana Zimmermann, 1780:129. Type locality "Bewohnt in grossen Heerben Carolina *v*), Virginien, Louisiana *w*), und geht vielleicht bis Panama *x*) hinunter"; restricted to Virginia by Hershkovitz (1948:43).

[*Cervus*] *virginianus* Boddaert, 1784:135. Type locality "Virginia." Preoccupied by *Dama virginiana* Zimmermann.

[*Cervus capreolus*] *Cariacou* Boddaert, 1784:136. Type locality "Gujania, Brasilia"; restricted to "Guyane, coastal French Guiana," by Hershkovitz (1948:44).

[*Cervus*] *mexicanus* Gmelin, 1788:179. Type locality "nova Hispania, Guiana et Brasilia"; restricted to the Valley of Mexico by Osgood (1902:88).

Cervus sylvaticus Kerr, 1792:303. No type locality given; based on Barrere's (1741:151) "Biche des Bois" from French Guiana.

Cervus cariacou Kerr, 1792:304. No type locality given; based on

Smellie's (1780) description of Buffon's (1764) "cariacou." Preoccupied by *Cervus capreolus cariacou* Boddaert.

Cervus campestris F. Cuvier, 1817:484. No type locality designated; based on antlers from Brazil figured by Daubenton (1756) and on a similar specimen ("qui se trouvait dans le cabinet de Tenon") without locality (Cabrera, 1941).

Corvus macrourus Rafinesque, 1817:436. Type locality "the plains of the Kansas river"; restricted to plains near Wakarusa Creek, Douglas Co., Kansas, by Miller and Kellogg (1955:804).

Cervus Nemoralis Hamilton-Smith, 1827a:137. Type locality "woody regions of tropical America, and, as it would seem, as far north as the southern parts of the United States." Type locality restricted to "Central America, round the Gulph of Mexico to Surinam" (Hamilton-Smith, 1827b:318); further restricted to "from Honduras to Panama" (Lydekker, 1915:170).

C[*ervus (Mazama)*]. *nemoralis*: Hamilton-Smith, 1827b:317. Name combination.

Cervus gymnotis Wiegmann, 1833:963. Type locality "stammt aus Columbien"; restricted to the Orinoco region, Venezuela, by Osgood (1914:138).

Mazama nemoralis: Jardine, 1835:175. Name combination.

Dorcelaphus macrurus: Gloger, 1841:40. Name combination.

Cariacus leucurus: Lesson, 1842:173. Name combination.

Cariacus mexicanus: Lesson, 1842:173. Name combination.

Cariacus nemoralis: Lesson, 1842:173. Name combination.

Cervus spinosus Gay and Gervais, 1846:93. Type locality "l'Amérique méridionale."

Cervus (Mazama) leucurus: Sundevall, 1846:181. Name combination.

C[*ervus*]. *savannarum* Cabanis, 1848:785. Type locality "British-Guiana."

Cariacus (?) spinosus: Gray, 1852:236. Name combination.

Cervus toltecus Saussure, 1860:247. Type locality "des environs d'Orizaba," Vera Cruz, Mexico.

Cervus gymnotus Gerrard, 1862:267. Incorrect subsequent spelling of *C. gymnotis* Wiegmann.

Coassus toltecus: Gray, 1872:92. Name combination.

Reduncina leucura: Fitzinger, 1874:357. Name combination.

Reduncina mexicana: Fitzinger, 1874:357. Name combination.

Reduncina nemoralis: Fitzinger, 1874:357. Name combination.

Reduncina savannarum: Fitzinger, 1874:357. Name combination.

Cervus (Coassus) peruvianus Gray, 1874:332. Type locality "Ceuchupate," Peru.

Cervus yucatanensis Hays, 1874:218. Type locality "throughout Yucatan and the southern part of Mexico."

Cariacus virginianus couesi Coues and Yarrow, 1875:111. Type locality "Camp Crittenden," Santa Cruz Co., Arizona.

Cervus acapulcensis Caton, 1877:113. Type locality "Acapulco," Guerrero, Mexico.

Cariacus peruvianus: Brooke, 1878:920. Name combination.

Cariacus savannarum: Brooke, 1878:920. Name combination.

Cariacus toltecus: Brooke, 1878:921. Name combination.

Gymnotis wiegmanni Fitzinger, 1879a:344. New name for *Cervus gymnotis* Wiegmann.

Cervus columbicus Fitzinger, 1879b:66. Type locality "Mittel-Amerika, Columbien, wo diese Form in der Republik Neu-Granada vorkommt."

Cariacus clavatus True, 1889:417. Type locality "extends at least from the province of Tehuantepec, in Mexico, to Costa Rica"; restricted to Segovia River, about 50 mi from the sea, Eastern Honduras, by Lyon and Osgood (1909:12).

Cervus brachyceros Philippi, 1894:10. Type locality "Cajamarca," Peru.

Cariacus virginianus mexicanus: Rhoads, 1894:524. Name combination.

Dorcelaphus couesi: J. A. Allen, 1895:200. Name combination.

Dorcelaphus virginianus macrourus: J. A. Allen, 1895:257. Name combination.

Cariacus osceola Bangs, 1896:26. Type locality "Citronelle, Citrus County, Florida."

Dorcelaphus texanus Mearns, 1898:23. Type locality "Fort Clark [north of Eagle Pass, on Big Bend of Rio Grande (Miller and Kellogg, 1955:803)], Kinney County, Texas."

Odocoileus thomasi Merriam, 1898:102. Type locality "Huehuetan, Chiapas, Mexico."

Odocoileus truei Merriam, 1898:103. Replacement name for *Cariacus clavatus* True, preoccupied by *Cervus clavatus* Hamilton-Smith.

Odocoileus nelsoni Merriam, 1898:103. Type locality "San Cristobal, highlands of Chiapas, Mexico."

Mazama [(*Dorcelaphus*)] *americana*: Lydekker, 1898:249. Name combination; not *Mazama americana* (Erxleben).

Mazama [(*Dorcelaphus*)] *americana typica* Lydekker, 1898:254. Type locality "Eastern North America, namely from Maine over much of the United States east of the Missouri river, typically from Virginia and Carolina, and probably as far south as Louisiana."

Mazama [(*Dorcelaphus*)] *americana macrura*: Lydekker, 1898:257. Name combination.

Mazama [(*Dorcelaphus*)] *americana osceola*: Lydekker, 1898:259. Name combination.

Mazama [(*Dorcelaphus*)] *americana couesi*: Lydekker, 1898:261. Name combination.

Mazama [(*Dorcelaphus*)] *americana texana*: Lydekker, 1898:261. Name combination.

Mazama [(*Dorcelaphus*)] *americana mexicana*: Lydekker, 1898:261. Name combination.

Mazama [(*Dorcelaphus*)] *americana tolteca*: Lydekker, 1898:263. Name combination.

Mazama [(*Dorcelaphus*)] *americana nemoralis*: Lydekker, 1898:264. Name combination.

Mazama [(*Dorcelaphus*)] *americana gymnotis*: Lydekker, 1898:265. Name combination.

Mazama [(*Dorcelaphus*)] *americana savannarum*: Lydekker, 1898:266. Name combination.

Mazama [(*Dorcelaphus*)] *americana peruviana*: Lydekker, 1898:267. Name combination.

Mazama [(*Dorcelaphus*)] *americana truei*: Lydekker, 1898:267. Name combination.

Mazama spinosa: Lydekker, 1898:280. Name combination.

Odocoileus couesi: Seton-Thompson, 1898:286. Name combination.

Odocoileus leucurus: Seton-Thompson, 1898:286. Name combination.

Odocoileus texanus: Seton-Thompson, 1898:286. Name combination.

Odocoileus americanus: Miller, 1899:299. Name combination.

Odocoileus americanus borealis Miller, 1900:83. Type locality "Bucksport, [Hancock County,] Maine."

Odocoileus costaricensis Miller, 1901:35. Type locality "Talamanca, on the eastern side of Costa Rica, between coast and the foot of the Cordilleras."

Odocoileus americanus macrourus: Miller and Rehn, 1901:14. Name combination.

Odocoileus osceola: Miller and Rehn, 1901:17. Name combination.

Odocoileus texensis Miller and Rehn, 1901:17. Incorrect subsequent spelling of *O. texanus* (Mearns).

Odocoileus americanus osceola: Elliot, 1901:40. Name combination.

Odocoileus toltecus: Miller and Rehn, 1901:117. Name combination.

Odocoileus virginianus louisianae G. M. Allen, 1901:449. Type locality "Mer Rouge, Morehouse County [=Parish], Louisiana."

Dama lichtensteini J. A. Allen, 1902:20. Replacement name for *Cervus mexicanus*, Lichtenstein, 1827:18, which J. A. Allen (1902) reported as preoccupied by *Cervus mexicanus* Gmelin.

Odocoileus virginianus borealis: Stone and Cram, 1902:39. Name combination.

Odocoileus louisianae: Stone and Cram, 1902:39. Name combination.

Odocoileus virginianus macrourus: Stone and Cram, 1902:39. Name combination.

Odocoileus mexicanus: Osgood, 1902:87. Name combination.

Dama rothschildi Thomas, 1902a:136. Type locality "Island of Coiba," Veraguas, Panama.

Odocoileus rothschildi: Thomas, 1902b:198. Name combination.

Odocoileus battyi J. A. Allen, 1903a:591. Type locality "Rancho Santuario, northwestern Durango," Mexico.

Odocoileus sinaloae J. A. Allen, 1903b:613. Type locality "Escuinapa, southern Sinaloa, Mexico."

Cariacus gymnotis Goeldi and Hagmann, 1904:87.

Odontocoelus americanus couesi: Elliot, 1904:70. Name combination.

Odontocoelus americanus texensis: Elliot, 1904:70. Name combination.

Odontocoelus battyi: Elliot, 1904:71. Name combination.

Odontocoelus lichtensteini: Elliot, 1904:72. Name combination.

Odontocoelus rothschildi: Elliot, 1904:72. Name combination.

Odontocoelus costaricensis: Elliot, 1904:73. Name combination.

Odontocoelus truii: Elliot, 1904:73. Name combination and incorrect subsequent spelling of *truei* Merriam, 1898.

Odontocoelus nemoralis: Elliot, 1904:74. Name combination.

Odontocoelus toltecus: Elliot, 1904:74. Name combination.

Odontocoelus nelsoni: Elliot, 1904:75. Name combination.

Odontocoelus thomasi: Elliot, 1904:75. Name combination.

Odontocoelus sinaloae: Elliot 1904:78. Name combination.

[*Odocoileus* (*Odocoileus*)] *philippii* Trouessart, 1905:706. Replacement name for *Cervus brachyceros* Philippi, preoccupied by *Cervus brachyceros* Gervais and Ameghino, 1880.

Odontocoelus americanus louisianae: Elliot, 1905:44. Name combination.

Odontocoelus americanus osceola: Elliot, 1905:44. Name combination.

Odontocoelus americanus macrourus: Elliot, 1905:44. Name combination.

Odocoileus rothschildi chiriquensis J. A. Allen, 1910:95. Type locality "Boqueron, Chiriqui," Panama.

Mazama americana borealis: Ward, 1910:104. Name combination.

Dorcelaphus americanus savannarum: Pocock, 1910:962. Name combination.

Odocoileus americanus louisianae: Miller, 1912:386. Name combination.

Mazama virginiana borealis: Lydekker, 1914:102. Name combination.

Mazama virginiana lichtensteini: Lydekker, 1914:103. Name combination.

Odocoileus lasiotis Osgood, 1914:136. Type locality "Paramo de los Conejos, Sierra de Merida, [Táchira,] Venezuela."

Odocoileus gymnotis: Osgood, 1914:138. Name combination.

Odocoileus spinosus: Osgood, 1914:138. Name combination.

Odocoileus columbicus: Osgood, 1914:139. Name combination.

Cariacus wisconsinensis Belitz, 1919:1. Proposed as a replacement name for *D. virginiana* of authors on supposition that species originated in Wisconsin.

Odocoileus lasiotus Sanborn, 1947:275. Incorrect subsequent spelling of *lasiotis*.

CONTEXT AND CONTENT. Content noted in generic summary above. Most authors recognize 30 subspecies of *O. virginianus* in North and Central America (Baker, 1984; Hall, 1981; Taylor, 1956); eight additional subspecies are recognized from South America (Halls, 1978; Mendez-Arocha, 1955).

O. v. acapulcensis (Caton, 1877:113), see above.

O. v. borealis (Miller, 1900:83), see above.

O. v. cariacou (Boddaert, 1784:136), see above (*cariacou* Kerr, *sylvaticus* Kerr, *campestris* Cuvier, *spinosus* Gay and Gervais, and *suaçuapara* Miranda-Ribiero, 1919, are synonyms).

O. v. carminis Goldman and Kellogg, 1940:81. Type locality "Botellas Cañon, Sierra del Carmen, northern Coahuila, Mexico (altitude 6,500 feet)."

O. v. chiriquensis (J. A. Allen, 1910:95), see above.

O. v. clavium Barbour and Allen, 1922:73. Type locality "Big Pine Key, Florida."

O. v. couesi (Coues and Yarrow, 1875:111), see above (*battyi* J. A. Allen is a synonym; *baileyi* Lydekker is a lapsus for *O. v. battyi*).

O. v. curassavicus (Hummelinck, 1940:65). Type locality "Island of Curaçao," Netherland Antilles.

O. v. dacotensis Goldman and Kellogg, 1940:82. Type locality "White Earth River, Mountrail County, North Dakota."

O. v. goudotii (Gay and Gervais, 1846:94). Type locality "vit dans les régions élevées de la Nouvelle-Grenade;" (*columbicus* Fitzinger and *lasiotis* Osgood are synonyms).

O. v. gymnotis (Wiegmann, 1833:963), see above (*savannarum* Cabanis, *wiegmanni* Fitzinger, and *tumatumari* J. A. Allen, 1915, are synonyms).

O. v. hiltonensis Goldman and Kellogg, 1940:83. Type locality "Hilton Head Island, Beaufort County, South Carolina."

O. v. leucurus (Douglas, 1829:330). Type locality "the districts adjoining the river Columbia, more especially in the fertile prairies of the *Cowalidske* and *Multnomah* River, within one hundred miles of the Western Ocean."

O. v. macrourus (Rafinesque, 1817:436), see above (*louisianae* G. M. Allen is a synonym).

O. v. mcilhennyi F. W. Miller, 1928:57. Type locality "near Avery Island, Iberia Parish, Louisiana."

O. v. margaritae (Osgood, 1910:24). Type locality "vicinity of Puerto Viejo, Margarita Island, Venezuela."

O. v. mexicanus (Gmelin, 1788:179), see above (*lichtensteini* J. A. Allen is a synonym).

O. v. miquihuanensis Goldman and Kellogg, 1940:84. Type loclaity "Sierra Madre Oriental, near Miquihuana, southwestern Tamaulipas, Mexico (altitude 6,500 feet)."

O. v. nelsoni (Merriam, 1898:103), see above.

O. v. nigribarbis Goldman and Kellogg, 1940:85. Type locality "Blackbeard Island, McIntoch County, Georgia."

O. v. oaxacensis Goldman and Kellogg, 1940:85. Type locality "mountains 15 miles west of Oaxaca, Oaxaca, Mexico (altitude 9,500 feet)."

O. v. ochrourus Bailey, 1932:43. Type locality "Coolin, south end of Priest Lake, Idaho;" (*ochrurs* Bailey, 1933, an incorrect subsequent spelling).

O. v. osceola (Bangs, 1896:26), see above (*fraterculus* Coues, 1896, is a synonym).

O. v. peruvianus (Gray, 1874:332), see above (*brachyceros* Philippi and *peruvianus* Cabrera are synonyms).

O. v. rothschildi (Thomas, 1902a:136), see above.

O. v. seminolus Goldman and Kellogg, 1940:86. Type locality "ten miles northeast of Everglades, Collier County, Florida."

O. v. sinaloae (J. A. Allen, 1903b:613), see above.

O. v. taurinsulae Goldman and Kellogg, 1940:87. Type locality "Bull's Island, Charleston County, South Carolina."

O. v. texanus (Mearns, 1898:23), see above (*texensis* Miller and Rehn and *texensis* J. A. Allen are incorrect subsequent spellings).

O. v. thomasi (Merriam, 1898:102), see above.

O. v. toltecus (Saussure, 1860:247), see above.

O. v. tropicalis (Cabrera, 1918:306). Type locality "La Maria, en el valle del Dagua," Colombia.

O. v. nemoralis (Hamilton-Smith, 1827a:137) see above (*truei* Merriam and *costaricensis* Miller are synonyms).

O. v. ustus (Trouessart, 1910:A26). Type locality "El Pelado, au nord de Quito (4,100ᵐ), sur la frontière de Colombie; Chillacocha, dans la Cordillère occidentale (3,800ᵐ), entre la ville de Machala et celle de Loja, province del Oro; Narihuiña, dans la Cordillère occidentale, au Nord de la montagne précédente (4,000ᵐ), entre Machala et Cuena, province de l'Azuay;" (*consul* Lönnberg, 1922, *abeli* Spillmann, *gracilis* Spillmann, *antonii* Spillmann, and *aequatorialis* Spillmann are synonyms).

O. v. venatorius Goldman and Kellogg, 1940:88. Type locality "Hunting Island, Beaufort County, South Carolina."

O. v. veraecrucis Goldman and Kellogg, 1940:88. Type locality "Chijol, northern Vera Cruz, Mexico (altitude 200 feet)."

O. v. virginiana (Zimmermann, 1780:129), see above (*wisconsinensis* Belitz is a synonym).

O. v. yucatanensis (Hays, 1874:218), see above.

DIAGNOSIS. The tail of *O. virginianus* is brown above, white below, and fringed with white laterally. *O. hemionus* has a black or white tail tipped with black. Ears of *O. virginianus* are about 50% the length of the head; in *O. hemionus* the ears are about 67% of the length of the head. The metatarsal gland is <25 mm long in *O. virginianus* and >25 mm in *O. hemionus*. Antlers of *O. virginianus* have one main beam from which tines arise vertically. Antlers of *O. hemionus* branch dichotomously and tines

FIG. 1. Adult male *Odocoileus virginianus macrourus* from Missouri. Photograph by M. Sullivan, Missouri Department of Conservation.

are about equal in size. Lachrymal fossae of *O. virginianus* are shallow compared to deep lachrymal fossae of *O. hemionus*.

GENERAL CHARACTERS. *O. virginianus* (Fig. 1) in the northern hemisphere undergo two complete molts per year and exhibit seasonal variation in pelage. The summer coat, acquired in May to June, consists of short, thin, wiry hairs and varies from red-brown to bright tan; the coat is darker along the mid-dorsum and paler on the face, throat and chest. The summer coat is replaced in late summer or early autumn by the winter coat which varies from blue-gray to gray-brown and has longer, thicker, and more brittle hairs. Adults have a white nose band, orbital region and throat patch. Each side of the chin bears a black labial spot (Guthrie, 1971). All underparts including lower tail, insides of legs, venter, and chin are white. Fawns have a reddish-brown coat with white dorsal spots that disappear at 3–4 months of age (Hesselton and Hesselton, 1982; Sauer, 1984).

Subspecies with larger body size occur at greater latitudes or higher elevations, whereas smaller subspecies occur at latitudes nearer the equator or lower elevations. External body measurements (in mm) of the largest male of each subspecis range as follows: total length, 1,041–2,400; length of tail, 100–365; length of hind foot, 279–538; height at shoulder, 533–1,067 (Taylor, 1956). Mass of adult males from the northern United States and southern Canada ranges from 90 to 135 kg and varies seasonally. Females weigh 20–40% less. Adult deer in the Florida Keys or from Coiba Island may weigh ≤22.5 kg (Halls, 1978). Within a subspecies, mass may vary up to 30% (Teer et al., 1965). Mass at birth ranges from 1.8 to 3.6 kg for North American subspecies; summer mass of adult females averages 45 kg and of adult males averages 68 kg. Shoulder heights average 91 cm for adult males and slightly smaller for adult females (Sauer, 1984). Condylobasal length of the skull for the largest male for each subspeceis ranges from 197.5 to 322.0 mm (Fig. 2; Taylor, 1956). Antlers are found on males (rarely on females) from April through February. Male fawns have small bumps or "buttons" the first year and unbranched "spikes" or branched antlers thereafter (Halls, 1978). Size and shape of antlers reflect age, nutrition (Sauer, 1984), and heredity and heterozygosity (Hesselton and Hesselton, 1982; Scribner et al., 1989).

DISTRIBUTION. White-tailed deer range from southern Canada throughout most of the coterminous United States (absent in Utah, rare in Nevada and California), southward to northern South America (Fig. 3). Historically, *O. virginianus* probably was not as abundant as today, but occupied nearly as wide a range. Numbers increased after land clearing and forest exploitation, but then were reduced as a result of overhunting. After World War II, a recovery was observed, presumably a result of forest rejuvenation,
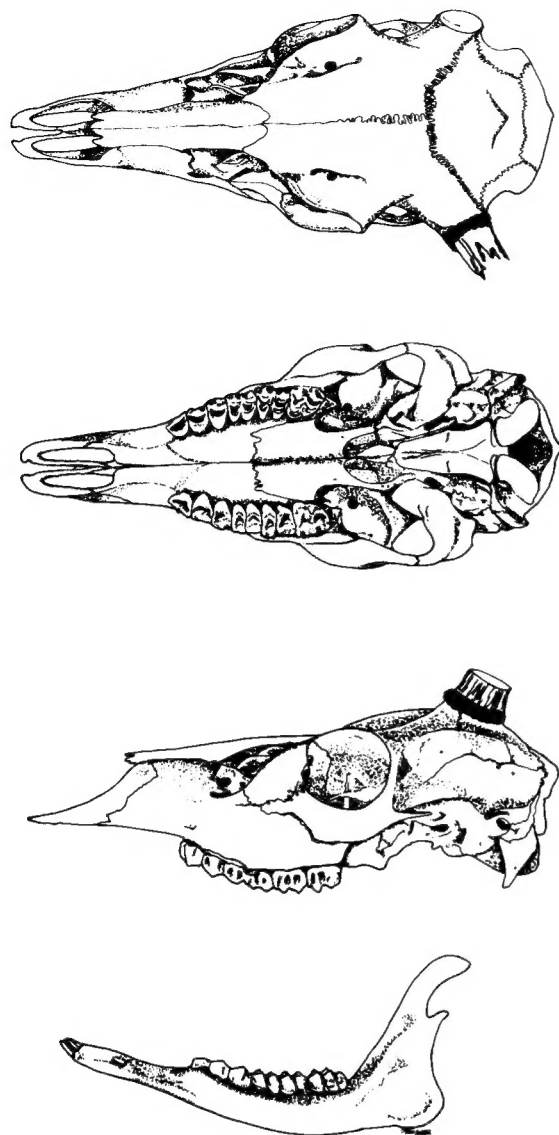
FIG. 2. Dorsal, ventral and lateral views of the cranium and lateral view of lower jaw of a male *Odocoileus virginanus texanus* from Encinal, LaSalle County, Texas (University of Kansas 16538). Greatest length of cranium is 288.35 mm. Drawing by K. M. Endres.
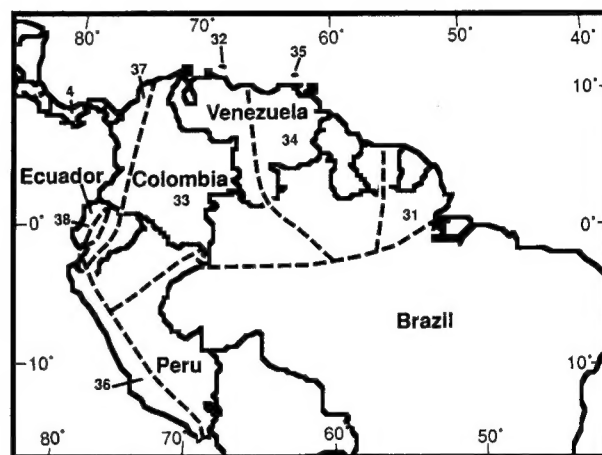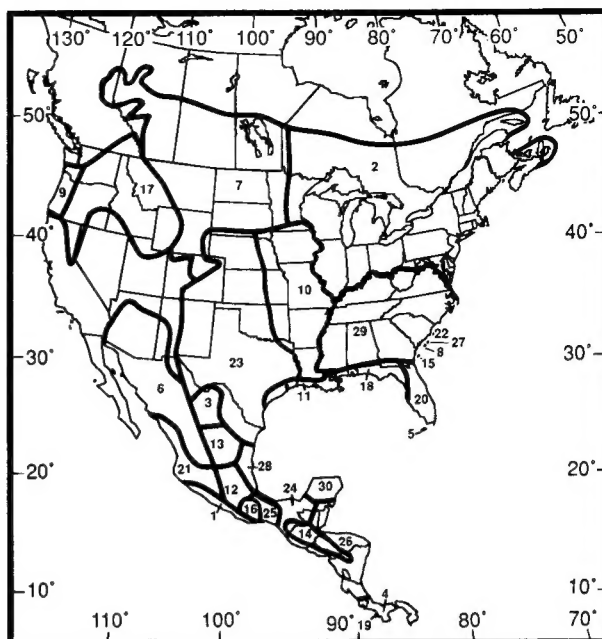

FIG. 3. Distribution of *Odocoileus virginianus* in: a, North America (Halls, 1984) 1, *O. v. acapulcensis*; 2, *O. v. borealis*; 3, *O. v. carminis*; 4, *O. v. chirquensis*; 5, *O. v. clavium*; 6, *O. v. couesi*; 7, *O. v. dacotensis*; 8, *O. v. hiltonensis*; 9, *O. v. leucurus*; 10, *O. v. macrourus*; 11, *O. v. mcilhennyi*; 12, *O. v. mexicanus*; 13, *O. v. miquihuanensis*; 14, *O. v. nelsoni*; 15, *O. v. nigribarbis*; 16, *O. v. oaxacensis*; 17, *O. v. ochrourus*; 18, *O. v. osceola*; 19, *O. v. rothschildi*; 20, *O. v. seminolus*; 21, *O. v. sinaloae*; 22, *O. v. taurinsulae*; 23, *O. v. texanus*; 24, *O. v. thomasi*; 25, *O. v. toltecus*; 26, *O. v. truei*; 27, *O. v. venatorius*; 28, *O. v. veraecrucis*; 29, *O. v. virginianus*; 30, *O. v. yucatanensis*; and b, South America (Whitehead, 1972) 31, *O. v. cariacou*; 32, *O. v. curassavicus*; 33, *O. v. guodotii*; 34, *O. v. gymnotis*; 35, *O. v margaritae*; 36, *O. v. peruvianus*; 37, *O. v. tropicalis*; 38, *O. v. ustus*.

enforcement of game laws, public support, and successful reintroductions (Baker, 1984; McCabe and McCabe, 1984).

Originally, *O. virginianus* was only in the southern parts of a few Canadian provinces. Forest cutting and burning, curtailment of prairie fires, and increased agriculture have allowed the extension of their range farther north into Canada. Populations are probably affected in northern marginal habitats by severe winters (Halls, 1978). Introductions of *O. virginianus* abroad have had varied success and include the British Isles, Czechoslovakia, Finland, Yugoslavia, New Zealand, Cuba, Virgin Islands, Curaçao, and other Caribbean Islands (Baker, 1984).

FOSSIL RECORD. *Odocoileus* appeared in the North America fauna at the beginning of the Blancan (early Pliocene) about 3.5 × 10⁶ years ago (Kurtén and Anderson, 1980). Members of this genus were the most common cervids in the Blancan and Pleistocene faunas of North America. *Procoileus edensis* (Frick) from the Eden Pliocene in California is a possible ancestor. *O. virginianus* appeared in the later Blancan about 2 × 10⁶ years ago, and probably was derived from the early Blancan *Odocoileus brachyodontus*. Its origin probably in "Middle America," the geographic expansion of *O. virginianus* toward greater latitudes was comparatively recent (Hershkovitz, 1972:363). *O. virginianus* was not uncommon in the central and eastern states during the Irvingtonian (early to mid-

Pleistocene) and was common and widespread in the Rancholabrean (late Pleistocene). Numerous remains at Holocene (Recent) occupation sites suggest *O. virginianus* was an important game animal to Paleo-Indians (Kurtén and Anderson, 1980).

FORM AND FUNCTION. Guard hairs of the summer coat are 1–3.5 mm in length and usually are shed in August and September (Jacobsen, 1973). Winter coat guard hairs are 5–27 mm in length and are shed in April, May, and June (Sauer, 1984). External glands include forehead glands (Atkeson and Marchinton, 1982), preorbital glands, interdigital glands, metatarsal glands, and tarsal glands that secrete pheromones, possibly governed by hormonal and sympathetic nervous stimulations (Sauer, 1984). Two pairs of mammae usually are present. There is little correlation

between prepartum diet and milk composition (Verme and Ullrey, 1984). Fat content at parturition ($\bar{X} = 10.3\%$) varies greatly among individuals and decreases to 8.1% by 21 days postpartum. Initially, the colostrum is rich in vitamin A ($\bar{X} = 66.6\ \mu g/100$ ml), but drops to 67% of this level in 3 days.

There are 32 teeth (i 0/3, c 0/1, p 3/3, m 3/3); the lower incisors are separated from the molariform teeth by a diastema (Sauer, 1984). Anomalies include limb abnormalities (Scanlon, 1974) and supernumeray teeth and other dental anomalies (Free et al., 1972; Krausman, 1978b; Wing, 1965). The ilia of the pelvis are broad and expanded and the humerus and femur are shortened and included in the body musculature (Sauer, 1984). Antler growth from pedicels on frontal bones is stimulated by an increase in prolactin, usually begins mid-March to April, and continues through August or September. Decrease in testosterone during December–January initiates a separation layer and antlers are cast (Mirarchi et al., 1978). Antlers in many southern areas are retained until spring (Sauer, 1973; Zagata and Moen, 1974); dominant males shed velvet earlier and retain antlers longer (Forand et al., 1985). With adequate nutrition, successive sets of antlers grow larger. Antler density and chemical composition varies with age and location within the antler with a tendency toward progressively lower density in older males; phosphorus, potassium, calcium, zinc, and aluminum increase whereas magnesium, manganese, sodium, strontium, and barium decrease with age (Miller et al., 1985).

Fat reserves, which are cued by photoperiod and controlled by the endocrine system, are highly variable, but may be a crude assessment of physical condition (Ransom, 1965). Mandibular or femur marrow (Verme and Holland, 1973), thymus (Ozoga and Verme, 1978), or total kidney fat (Monson et al., 1974) may be used to assess nutritional status. Nutritional status declines winter through summer and is greatest in autumn (DeLiberto et al., 1989).

ONTOGENY AND REPRODUCTION. Ovulation occurs 12–14 h after estrus. Fertilization occurs in the fallopian tube; implantation occurs 30 days after conception (Verme and Ullrey, 1984). Mean gestation is about 202 days (Halls, 1978), but differs among subspecies and ranges from 187 to 222 days (Haugen, 1959; Verme and Ullrey, 1984). Organ differentiation in the prenate is apparent at 37 days (Armstrong, 1950). The fetus is about 200 mm in length and 300 g in mass at midterm (Short, 1970), and about 500 mm and 3 kg at 180 days (Verme, 1963). Females with inadequate diets catabolize fat, bone, and body tissue to nourish the fetus (Ullrey et al., 1970). In utero productivity increases with improved nutrition (Ozoga and Verme, 1982).

Neonatal mass and mortality are closely related to maternal nutrition and weather severity (Verme, 1977). Postpartum mass is greater and survival higher for fawns whose mothers received better nutrition. Litter size ranges from one to three and is related to genetic factors and nutrition (Verme and Ullrey, 1984), but is not greatly influenced by intense social pressure (Ozoga et al., 1982).

Neonates nurse immediately and on average gain 0.2 kg/day initially, doubling in weight by about 2 weeks and tripling in weight within 1 month (Verme, 1963). Growth is related to adequate nutrition (Teer et al., 1965; Ullrey et al., 1967). Two rows of spots that range from 272 to 342 and average 0.6–1.3 cm in diameter occur along each side of the spine from the tail to the ears (Severinghaus and Cheatum, 1956). The spotted pelage is lost with the molt in August and September. Neonates have four incisors. Remaining milk teeth grow during the first few weeks; permanent teeth erupt by 9–10 months (Sauer, 1984). Fawns begin grazing when a few weeks old and are functional as ruminants by 2 months (Short, 1964). Nursing may continue into autumn, but weaning typically occurs by 10 weeks postpartum (Marchinton and Hirth, 1984).

Females can breed at 6–7 months of age or about 36 kg, but usually not until 1.5 years old. Males attain sexual maturity by 1.5 years of age (Halls, 1978); puberty seems to be governed by physiological state (Verme and Ullrey, 1984), which is influenced by nutritional plane (Ozoga and Verme, 1982). Breeding activity of females is influenced by the presence of a mature rutting male (Verme et al., 1987), physical condition, and genetics. The ultimate determinant of breeding season is availability of adequate nutrition, which is cued by photoperiodism (Verme and Ullrey, 1984). Throughout their range, females generally come into estrus in autumn (Sauer, 1984). Ovulation occurs during a "silent heat," when no distinct signs are apparent, 12–23 days before a physiological heat when mating occurs (Plotka et al., 1977). Females are receptive

for about 24 h and typically come into heat 1–2 times again at 21–30-day intervals if not inseminated (Haugen, 1959; Plotka et al., 1977). Pen-reared females undergo up to seven cycles, with increasing length, in the presence of a mature male (Knox et al., 1988). Life expectancy may exceed 20 years, but few live more than 10 years (Halls, 1978). Life expectancy is 2.5 years in Illinois (Calhoun and Loomis, 1974) and 2 years for males and 3 years for females in Pennsylvania (Forbes et al., 1971). Proximate causes of death include fence entanglement, automobile accidents, disease, parasites, predation, hunter crippling, old age, and poaching (Halls, 1984).

ECOLOGY. White-tailed deer inhabit a wide range of habitats from north-temperate to subtropical and semi-arid environments in North America and include rainforests and other equatorial associations of Central America and northern South America. Greatest abundance is east of the Mississippi River, especially within the coastal wetlands and islands along the Gulf of Mexico and Atlantic seaboard (McCabe and McCabe, 1984).

Abundance and distribution of *O. virginianus* have both increased somewhat since early historic times when an estimated 40 million deer occupied 7.8 million km² in the United States and Canada (McCabe and McCabe, 1984). *O. virginianus* has benefitted from the mosaic of second-growth forest, openings, and farmlands created by logging, clearing, and agriculture. These activities have seemingly mimicked many natural distrubances (i.e., fire, blowdown) that retard succession and provide forest openings and early successional habitats (McCabe and McCabe, 1984). Irrigation encouraged extension of the range into west Texas and other arid regions of the Southwest; clearcutting increased the quantity and quality of available forage and permitted this species to inhabit previously unoccupied portions of northern boreal forests. Conversion of forests to short-rotation, even-aged monocultural stands, however, reduces the quantity and quality of food (Newsom, 1984).

Ecological limitations in northern or montane habitats are related to depth, quality, and duration of snow (Blouch, 1984). Extensive snow cover restricts mobility and forage availability and influences habitat use (Wishart, 1984), all of which affect energy budgets of white-tailed deer (Telfer and Kelsall, 1984) and contribute to overwinter mortality (Fuller, 1990). During mild winters, they occupy open-canopied shrublands of southeastern British Columbia and aspen parklands in Alberta; when snow cover is >30–40 cm, they are forced into denser-forested regions where forage often is depleted and survival and reproduction is low (Wishart, 1984). In the hardwood and boreal *Picea–Abies* forests of the Northeast and Great Lakes region, white-tailed deer concentrate in "yards" where coniferous forests intercept as much as 50% of the snowfall (Blouch, 1984).

In more southern latitudes and lower elevations, the amount and temporal distribution of precipitation also impose ecological limits (Evans, 1984; Mendez, 1984); *O. virginianus* favor more mesic climates and vegetation within arid regions. In the southwestern United States, most of its range received >25 cm of precipitation annually with the greatest densities occurring where annual totals average about 40 cm. Riparian deciduous forests and montane woodlands are habitat islands with riparian zones serving as corridors of movement and dispersal within an otherwise unsuitable environment (Evans, 1984; Smith, 1982). Distribution and abundance throughout the Great Plains are limited by the quantity and quality of vegetative cover (Dusek et al., 1989; Menzel, 1984).

Carrying capacity of habitats varies greatly among ecological regions, but density of *O. virginianus* is directly related to number and distribution of forest openings. Climax *Picea–Abies* forest in the Northeast and other mature forests support comparably few white-tailed deer. In less forested regions, their distribution and density varies directly with abundance of riparian and other woody cover (Smith, 1987a; Dusek et al., 1989). Local densities in oak-savannas of interior valleys of southwestern Oregon approach 34 white-tailed deer/km² in ≥50% forest cover (Smith, 1987a). Availability of agricultural crops improves habitat quality; intensively managed wildlife areas (numerous, small agricultural plots) in *Quercus–Carya* forests can support 80/km² (Torgerson and Porath, 1984). Aspen (*Populus*) parklands in southern Alberta are prime habitat supporting 12/km². The edge along aspen forest and grassland is dense with shrubs and forbs, prime forage for deer. Optimum habitat in Alberta consists of 65% woodland, 20% grassland, and 15% mixed cropland and water; areas with <35% aspen cover are un-

suitable overwintering habitat (Wishart, 1984). Bottomland hardwoods produce the highest quality food in the Coastal Plain, supporting a mean of 25 white-tailed deer/km². Distribution in the more arid lands are patchier and densities are seldom >4/km² (Cook, 1984; Evans, 1984; Menzel, 1984).

South of the Rio Grande, *O. virginianus* is most abundant in mixed pine–oak forests of Mexico and in second-growth forests and thickets and forest–savanna ecotones of Guatemala, Honduras, Belize, El Salvador, Costa Rica, and Panama. This species also is common in the pine savannas and forests of Belize and Nicaragua (Mendez, 1984). Savannas also are primary habitat in South America. These continuous grasslands have palms and other fruit trees scattered throughout on wetter sites (high savannas) and mesquite (*Prosopis*) and other chapparal-like vegetation on drier low savannas (Brokx, 1984).

White-tailed deer occupy a well-defined home range year after year (Staines, 1974), but they are not territorial. Individuals will defend bedding sites (Gavin et al., 1984) and limited resources (Ozoga, 1972; Smith, 1984) and tending males will defend estrous females. Movements and home range are influenced by age, sex, density, social interactions, latitude, season, and habitat characteristics. Size of home range varies inversely with density and vegetative cover (Marchinton and Hirth, 1984) and habitat diversity (Verme, 1973). Annual home range of sedentary populations averages 59–520 ha and areas of seasonal use rarely exceed 1.6 km in radius. Linear home ranges are typical and represent the most efficient configuration for using resources in patchy environments (Marchinton and Hirth, 1984). Circular home ranges with uniform use characterize more homogeneous habitats (Inglis et al., 1979).

Yearlings move farther and more frequently than other age classes, whereas males move farther and occupy larger home ranges than females (Gavin et al., 1984; Sparrowe and Springer, 1970), especially during the rut (Smith, 1982). Fawns exhibit the smallest movements (Garner and Morrison, 1977) and occupy the smallest ranges (Smith, 1982). Dispersal rates also vary among age-sex classes; annual rates (in percent) reported for Crab Orchard National Wildlife Refuge, Illinois, averaged 4, 7, 10, 13, and 80 for fawns, adult females, adult males, yearling females, and yearling males, respectively (Hawkins et al., 1971). Social pressures associated with competition among males during the rut (Marchinton and Hirth, 1984) and among femaels for fawning habitat (Dusek et al., 1989) serve as the primary impetus for dispersal. White-tailed deer in northern temperate areas have larger and less stable home ranges than those in southern latitudes (Sparrowe and Springer, 1970). Seasonal migrations averaging 15.6–23.2 km are common in northern and montane populations (Marchinton and Hirth, 1984). Winter migrations are a response to cold and a sudden drop in temperature (Hoskinson and Mech, 1976); return to summer range occurs as forage becomes available (Verme, 1973). Summer ranges are traditional, but winter range may vary annually according to depth of snow (Mattfield et al., 1977). Females and young move directly between seasonal ranges; adult males meander (Rongstad and Tester, 1969).

Seasonal shifts in the center of activity occur in response to local changes in food availability (Byford, 1970), cover and water (Smith, 1982), interaction with livestock (Suring and Vohs, 1979), and predators (Mech, 1977; Nelson and Mech, 1981). In Michigan, females show greater dispersion than males; seasonal use of habitat differs between sexes with the greatest overlap during winter and the least during fawning (McCullough et al., 1989).

White-tailed deer allocate more time to feeding than any other activity and often forage while moving to and from feeding areas. They select the most nutritious forage available (McCullough, 1984). In xeric habitats, succulents constitute as much as 70% of the total diet during dry seasons (Krausman, 1978a). Generally, grasses and forbs dominate the diet during spring and early summer, and use parallels the annual cycle of herb production (Smith, 1982). As herbaceous vegetation matures, they switch to succulent, new-growth leaves and twigs. During autumn, soft and hard mast predominate in the diet, including fruits of *Fagus grandifolia, Smilaz, Crataegus, Diospyros virginiana, Vaccinium, Rhus, Vitis, Rubus,* and *Pyrus.* Where available, acorns (*Quercus*) are the most often selected food during autumn (Halls, 1984).

Winter diets are determined largely by availability. Dried leaves of deciduous trees, sedges, grasses, mushrooms and other fungi, and woody browse comprise a large proportion of the diet (Halls, 1984). Although highly available, woody browse is used infrequently in hardwood forests unless winters are severe and other foods are unavailable. In the northern Great Lakes states and portions of Canada, browse is the primary source of food because it is the only food available for nearly one-half the year (Blouch, 1984). When snow cover occurs, white-tailed deer abandon masts and herbaceous forage and feed almost entirely on woody browse of evergreens. *Thuja occidentalis, Acer rubrum, Tsuga, Pyrus americana, Cornus, Salix, Lonicera, Amelanchier,* and *Symphoricarpus albus* are selected browse species for northern forest regions (Coblentz, 1970; Halls, 1984).

In agricultural areas, farm crops are an important year-round source of food representing up to 78% by mass of the total diet (Gladfelter, 1984). Corn, soybeans, and alfalfa are heavily used during the growing season throughout midwestern and southeastern agricultural regions. Through autumn and winter white-tailed deer use the grain residue remaining after crop harvests. In the central and southern plains, woody browse is virtually replaced by farm crops with an much as 51% of the annual diet comprised of corn, wheat, alfalfa, and other grains where farms are adjacent to suitable cover. Many regions experience heavy use of orchards and nurseries. Depredation can be severe and landowner tolerance often is a primary consideration in managing white-tailed deer. Many states offer incentives to encourage legal harvests of either sex (Gladfelter, 1984).

Dynamics of populations vary greatly according to local environments. Mortality is biased according to age and sex; type and intensity of mortality determines age and sex structure and ultimately reproductive capacity of populations. Two major influences are seasonality and hunting. In severe environments, hunting removes animals that would otherwise succumb to natural winter mortality, but hunting mortality becomes increasingly additive (i.e., increases total mortality) in milder climates or where deer overwinter on a high nutritional plane (Dusek et al., 1989). In Michigan's lower peninsula, intensive hunting reduces the survival of males from 0.70 to 0.28 (Hayne, 1984); in eastern Montana hunting was more additive in females than males (Dusek et al., 1989). In north-central Minnesota, restricting harvest of anterless deer and limiting road access to hunters reduced hunting mortality. Varying hunting pressure potentially has the greatest influence on rates of population change; significant increases in population, however, are more likely to result from simultaneous changes in several demographic parameters (Fuller, 1990).

Nonhunted populations have an older age structure because of reduced adult and higher fawn mortality (Smith, 1982). Males experience greater mortality rates (0.40) compared to females (0.20) because of stresses of rut (Gavin, 1979). Proximate mortality includes vehicle collisions (44.2%), malnutrition (43.3%), predation (5.0%), parasites and disease (4.2%), and fence entanglement (3.3%—Smith, 1982). Yearlings were most susceptible to vehicle collisions while most predation occurred on fawns. Disease and parasites reduce reproductive success by influencing behavior and increasing susceptibility to other mortality factors (Davidson et al., 1981).

Populations of *O. virginianus* are capable of increasing exponentially and approach unimpeded instantaneous rates of increase ($r = 0.516$) at low densities, even in relatively poor habitat (McCullough, 1984). In excellent habitat, females reproduce as fawns, yearlings typically have twins, and triplets are common among adults. Reduced forage availability effects a density-dependent response in population growth by influencing age-specific natality and survivorship (Woolf and Harder, 1979), then fawn mortality, and finally mortality of the "residual population" (McCullough, 1984). Increasing density also increases social pressures among females and reduces fawn-rearing success (Dusek et al., 1989). As density decreases and resource availability increases, populations recover by decreased fawn mortality and increased natality. Duration of the recovery depends on how far the population exceeds carrying capacity and the consequent impact on vegetation (McCullough, 1984).

Populations that remain near the carrying capacity show the greatest fluctuation because the residual population is larger than a comparable population maintained below carrying capacity. Even at high densities, adult females attempt to reproduce and, if environmental quality is good, a large number of recruits is added. In poor years, recruitment is low and residual mortality will be high. Thus, in circumstances where the residual population does not experience unnatural, perennial mortality (e.g., nonhunted populations), stability is a function of habitat constancy and environmental harshness. Populations typically fluctuate widely because of the temporary nature of early successional habitats and decreasing availability of

nutritious forage. White-tailed deer occupying stable habitats can remain at equilibrium densities (Gavin et al., 1984).

Historically, *Canis lupus* and *Felis concolor* were the primary predators of white-tailed deer; *Lynx rufus*, *Ursus americanus*, *U. arctos*, and *Canis latrans* probably were incidental predators, concentrating on fawns. Today, domestic dogs are the most widespread predators (especially in the southeastern United States) of white-tailed deer, particularly fawns, pregnant females, and malnourished deer (Mech, 1984).

Where wolves and white-tailed deer coexist, wolf predation is the primary cause of natural mortality and influences deer behavior, social organization, and distribution (Nelson and Mech, 1981). Wolves each consume the equivalent of 15–20 adult deer/year (Mech, 1984). During summer, wolves prey mostly on fawns; older deer are most susceptible during migrations and on winter range. Wolves can exterminate local populations and account for most of the natural mortality on winter range, but white-tailed deer generally are not limited by predation (Nelson and Mech, 1981).

Coyotes have become significant predators of white-tailed deer and may be responsible for 80% of fawn mortality and 40% reduction in annual recruitment (Beasom, 1974; Cook et al., 1971). Removal of coyotes leads to an increase in local numbers of white-tailed deer. Even where coyote densities are too low to exert regulation, added noncompensatory mortality reduces density of local white-tailed deer populations (Mech, 1984).

White-tailed deer are sympatric with mule deer in 17 western states and three Canadian providences as far east as eastern Nebraska and south to central Mexico. Historically, direct contact was minimized because white-tailed deer occupied more mesic climates with brushy and woodland cover and mule deer used more open, xeric habitats. Each specis excluded the other from parts of the range where it was competitively superior (Smith, 1987*a*).

Extensive overgrazing, agriculture, and other land-use practices following European settlement altered native habitat and brought the species into sympatry where previously their ranges were parapatric (Anthony and Smith, 1977). Mule deer expanded their range where dense woodlands and brushlands were replaced by open grasslands (Anthony and Smith, 1977; Krausman, 1978*a*). Land-use practices that promoted establishment of brushlands and woody cover facilitated expansion of white-tailed deer into exclusive mule deer range (Wiggers and Beasom, 1986). Currently, spatial, habitat use, and forage overlap are considerable in many portions of recently established sympatric ranges (Smith, 1987*a*).

In montane regions of western Canada, *O. virginianus* is sympatric with *Ovis canadensis*, *Cervus elaphus*, *Alces alces*, *Oreamnos americana*, and mule deer. Segregation occurs according to aspect, slope, vegetational heterogeneity, and protein concent of grasses. During winter, white-tailed deer use relatively homogeneous plant communities with a high degree of overstory crown cover; spring habitats have a southerly to southwesterly aspect and support grasses with average protein content (Hudson, 1976).

Ranges of *O. virginianus* and *Alces alces* also overlap in second-growth boreal forests of Novia Scotia, New Brunswick, Quebec, Ontario, Maine, New York, and Minnesota. Extensive logging promoted expansion of *O. virginianus* into the traditional range of *A. alces*. In many areas, *O. virginianus* replaced *A. alces* as the dominant cervid. *Parelaphostrongylus tenuis*, a parasitic nematode enzootic in populations of *O. virginianus* in eastern North America, contributes to the decline of *A. alces* where the two cervids are sympatric (Anderson, 1972).

Size, structure, and interspersion of northern coniferous and deciduous-coniferous forest openings determine the amount of overlap in seasonal use of habitat. Little spatial overlap occurs during summer. Segregation also occurs in winter, much of which is altitudinal and related to snowcover. *A. alces* selects habitats according to food abundance, whereas *O. virginianus* selects shelter. Distribution of *O. virginianus* was positively related to basal area and density of trees (Kearney and Gilbert, 1976). In northeastern Minnesota, both species heavily utilized recent burns, especially summer to fall, and aquatic communities from May to June (Irwin, 1975). Competition for winter browse can be intense because of limited winter ranges and similarity in forage selection (Ludewig and Bowyer, 1985).

BEHAVIOR. *O. virginianus* typically is crepuscular, but varies activity according to several environmental variables (Mar-

chinton and Hirth, 1984) including human disturbance (Kammermeyer, 1975). *O. virginianus* is most active at low relative humidities (Hawkins and Klimstra, 1970) and intermediate barometric pressures (Thomas, 1966). Feeding activity increases prior to rain or snow storms, but the individual effect of wind, cloud cover, or precipitation is unclear (Progulske and Duerre, 1964). No consistent relationship between activity and moon phases has been reported (Carbaugh et al., 1975; Zagata and Haugen, 1974).

White-tailed deer are gregarious with two basic social groups: family groups centered around a matriach with females (fawns of previous generations) and their fawns and fraternal groups made up of adult and occasionally yearling males (Hawkins and Klimstra, 1970). Mixed groups of adult females and males occur, but social contact between sexes typically is restricted to the mating period. Mixed feeding groups may include deer of various age and sex, but these assemblages are temporary and represent aggregations rather than social groups. Family groups remain together year around except during fawning when younger females and fawns of the previous year join mixed feeding groups. Adult females may feed with other deer, but the family group in summer consists of a female with her fawns (Hardin et al., 1976; Hawkins and Klimstra, 1970; Hirth, 1977). Fawns begin to accompany their mother at 3–4 weeks postpartum; by 8 weeks of age, fawns are regular members of female groups. Yearling females rejoin adult females and fawns in the fall and remain as a family unit until the following fawning season; yearling males join adult male groups or form temporary associations with other yearling males (Hirth, 1977). Adult male–fawn associations are rare (Smith, 1984). Males are more social than females but the social unit is less stable; two to five males of various ages travel together, especially during winter to summer (Hirth, 1977). Males are solitary during the rut except when pursuing or tending estrous females. Little interaction occurs within male groups; mutual grooming (Forand and Marchinton, 1989) and dominant-subordinate interactions are most common (Marchinton and Hirth, 1984). Grooming occurs in all social groups and is directed at the head and neck (Forand and Marchinton, 1989; Hirth, 1977).

Social organization and behavior vary in relation to habitat (Hirth, 1977) and intensity of predation (Nelson and Mech, 1981). Group size is inversely related to density of cover. In dense woodlands, family groups seldom include more than one adult female, her current year's fawns, and female offspring of previous years; larger, multi-family groups are common in open brushland savannas. Inhabitants of dense woodlands show little inclination to alter group size or composition according to density of cover and are most aggressive and least tolerant of intruders. In open savanna, rates of social interaction for *O. virginianus* are 10–100 times less than in dense woodland and mixed feeding groups of all age and sex classes are common during all seasons (Hirth, 1977). Dispersion, social structure, and behavior may be a result of intense selective pressure to reduce predation from wolves (Nelson and Mech, 1981). The relationship between habitat and group size and composition also may have evolved as an adaptation to reduce predation (Hirth, 1977). Social grouping spreads the risk of predation throughout the group and use of traditional summer and winter ranges allows deer to take advantage of "buffer zones along the edges of wolfpack territories" (Nelson and Mech, 1981:44).

Dominance hierarchies typically exist and influence the behavior of individuals (Marchinton and Hirth, 1984). The matriarch is dominant in family groups; rank of remaining members is according to age (Townsend, 1973). Rank in male groups and multi-family groups also is influenced by size and physical condition (Hirth, 1977). In mixed groups, age–rank relationships persist with adult males dominating adult females and yearling males dominant over yearling females, especially during the rut (Townsend, 1973). Dominance hierarchies minimize conflict and overt aggression within groups (Hirth, 1977), and reduce energy expenditure and risk of injury (Marchinton and Hirth, 1984).

Social rank is conveyed through subtle postures, movements, and other behaviors that eliminate the need for continued "direct 2-way" interactions (Hirth, 1977:28). Subordinates typically avoid direct eye contact with dominants and move aside when approached directly. In response to stereotyped low-level aggression (example, hard look-ear drop; Hirth, 1977:22–23), subordinates display bathetic submissive behaviors (Hirth, 1977; Thomas et al., 1965). Only when dominance is uncertain (for example, in mixed feeding groups) do encounters result in direct aggression. During the breeding season, unresolved dominance among mature males results in one

or more stereotyped behaviors directed at the antagonist (Hirth, 1977).

Marking and rubbing behaviors are an integral part of social interactions, especially during the mating season (Moore and Marchinton, 1974). "Buck rubs" and scraping are visual and olfactory signposts displayed primarily by older males to establish dominance and facilitate intersexual communication (Kile and Marchinton, 1977). The forehead of males contains sudoriferous glands that are most active in dominant males during the rut (Atkeson and Marchinton, 1982). Together with secretions from the preorbital gland and saliva, males mark overhanging branches, twigs, and the bark of small saplings and stems with their head and antlers. Rubs are clumped spatially with each tree having one discrete rub; small (<2 cm) trees with smooth bark and the first branch high above the ground ($\bar{X}$ = 94.2 cm) are used most often (Benner and Bowyer, 1988). Rubbing is most intense during and just after velvet removal, continuing through the breeding season (Marchinton and Hirth, 1984). Density and location of rubs are determined by density of $\geq$2.5-year-old males, habitat, topography, food availability, and social mechanisms (Miller et al., 1987).

Scraping behavior has been observed in females (Sawyer et al., 1982) but occurs most often in dominant males $\geq$3.5 years old (Miller et al., 1987) during or just prior to peak breeding periods (Kile and Marchinton, 1977). "Rub-urination," combining urine with secretions of the tarsal gland, often is associated with scraping behavior (Hirth, 1977). Scrapes are visited regularly and facilitate communication between estrous females and males during the breeding season (Kile and Marchinton, 1977). Rub-urination probably provides information about male condition and rank to both estrous females and other males; synchrony of estrous females may be its adaptive function (Coblentz, 1976).

White-tailed deer make 13 distinguishable vocal and non-vocal sounds associated with specific intraspecific and interspecific interactions (Marchinton and Hirth, 1984; Richardson et al., 1983). "Bawls" are nonspecific distress calls given by deer of all age classes and sex during traumatic situations. The footstomp and alert-snort are frequently emitted by yearling and older white-tailed deer and often occur simultaneously or in sequences when they become aware of a predator or other intruder. Snort-wheeze and aggressive snort are emitted during disputes over rank, especially between males. The grunt is given by yearling and older individuals during dominant–subordinate interactions (most often by males) and as a cohesive call most often by females (Richardson et al., 1983). Sawyer (1981) reported a bleating, contact call used by members of a group when separated. Three additional grunts and a flehmen sniff, a low intensity inhaling sound associated with the investigation of female urine during the breeding season, have been described (Atkeson et al., 1988).

Females make a low grunt to call their fawns such as in the initiation of a nursing bout. Fawns respond with a soft, high-pitched mew or with higher intensity, more insistent bleats. The nursing whine, emitted by fawns while suckling, may serve to identify the fawn and reinforce the maternal bond. The bleat also is a vocalized cohesive call and appears to solicit maternal care; adult females other than the fawn's mother often respond to bleats (Marchinton and Hirth, 1984).

In response to bleat solicitations, females come quickly to aid their fawns and exhibit various defensive behaviors. Type and intensity of behavior may vary among years according to physical condition of females and their fawns and among age classes within a year (Smith, 1987b); older females recruit more fawns (Mech and McRoberts, 1990). Varying the type and intensity of maternal defense may be an important behavioral adaptation, allowing reproductive females to invest the greatest time and energy during seasons when the probability of success is greatest (Smith, 1987b).

White-tailed deer use various behaviors to avoid predation ranging from remaining motionless (Marchinton and Hirth, 1984) to group cohesion (Nelson and Mech, 1981) and flight behavior. Young fawns (especially $\leq$1 week old) respond to intruders with a dramatic decrease in heart rate, "alarm bradycardia," and reduced movements and sounds associated with normal or excited breathing and heart rates (Jacobsen, 1979). As fawns age, flight becomes the primary means of escaping predation. Individuals in flight erect and "flag" a conspicuous white tail which also exposes a large white rump patch. The behavior, exhibited most often in open habitats by young fawns and single individuals, serves primarily to reduce the risk of predation on neonates (Smith, 1991), and secondarily as a generalized "cohesive signal that helps to keep individuals in groups for antipredator benefits" (Hirth and McCullough, 1977:41).

GENETICS. The X chromosome is submetacentric and the Y chromosome is metacentric (Hsu, 1967). Autosomes include two submetacentrics and 66 acrocentrics or telocentrics (2n = 70, FN = 70). Invariant loci in *O. virginianus* are generally invariant in other mammals except for albumin. A large proportion of *O. virginianus* are polymorphic at the sorbitol dehydrogenase locus, whereas very few 6-phosphogluconate dehydrogenase or albumin heterozygotes have been observed (Baccus et al., 1977; Smith et al., 1984).

White-tailed deer exhibit the most genetic variability of large, grazing mammals (Breshears et al., 1988), which may partially explain the almost ubiquitous distribution of the species in the western hemisphere (Nevo, 1978). Of 35 loci, 27 were polymorphic (Smith et al., 1984). This is unusually high for mammals and contrary to that expected for large, endothermic mammals (Selander and Kaufman, 1973). Albinism is recessive and rarely occurs; melanism occurs less often (Smith et al., 1984).

Electrophoretic studies of *O. v. nigribarbis*, *O. v. texanus*, *O. v. borealis*, *O. v. osceola*, *O. v. seminolus*, and *O. v. virginianus* did not reveal significant genetic differentiation among subspecies (Smith et al., 1984). Genetic variability, however, differs significantly among populations; heterozygosity values in Georgia and South Carolina varied more than the number of alleles per locus and proportion of polymorphic loci (Smith et al., 1984). Allele frequencies exhibit significant temporal fluctuations within panmictic populations and differ (by an order of magnitude) among local populations and among age and sex classes within populations (Ramsey et al., 1979). Differences increase over distance and through time (Smith et al., 1984) and may be associated with variation in habitat quality (Dapson et al., 1979). Reproductive rates of females (Smith et al., 1984), fetal growth (Cothran et al., 1983), and gonadal development in fawns are associated positively with mean heterozygosity (Urbston, 1976). Fetal growth rate is related to mean heterozygosity of both mother and fetus and is attributed to differences in inbreeding. Inbreeding probably is a result of social structure (Cothran et al., 1983).

Hybridization has occurred between sympatric *O. virginianus* and *O. hemionus* in Washington and Texas (Carr et al., 1986; Gavin and May, 1988; Stubblefield et al., 1987). In captivity, the two species produced viable offspring, but the majority were sterile. One hybrid female bred with her father (*O. virginianus*) and produced a fertile, second-filial generation female (Cowan, 1962).

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W. P. SMITH, SOUTHERN HARDWOODS LABORATORY, U.S.D.A. FOREST SERVICE, SOUTHERN FOREST EXPERIMENT STATION, P.O. BOX 227, STONEVILLE, MISSISSIPPI 38776.